Morphology and natural history of the Land Mullet *Egernia major* (Squamata: Scincidae)

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ABSTRACT

The external morphology and osteology of the Land Mullet *Egernia major* is described based on all available material in Australian museum collections and extant type material. The complex nomenclatural history of this species is discussed. Multivariate analysis of variation in external morphology does not identify any segment of the geographic distribution as distinct, although there is some clinal variation. Available data do not provide evidence for a close relationship with any other *Egernia* species and the previously identified "*Egernia major*" species group is concluded to have no morphological support. Litter sizes of 3–7 are recorded and reproduction is vernal. The species is omnivorous, with a high frequency of fungi and nocturnal invertebrates in the stomach contents.

INTRODUCTION

Despite their formal description over a century ago, their familiarity to herpetologists and the ease and frequency with which they are kept in captivity, many of the large skinks in the genera *Egernia* and *Tiliqua* remain poorly studied. In particular, there is a paucity of information on basic life history, diet and distribution. Further, the systematics of these large species has rarely been explored subsequent to the initial description, which was almost always brief (even for the standards of the time), and based on only one or two specimens. The lack of data on these large skinks has hampered understanding of their phylogeny and conservation status.

The availability of increased samples of the large *Egernia* and *Tiliqua* in museum collections allows some correction of these deficiencies. This paper, the first in a projected series on the large *Egernia* species, uses museum specimens to redescribe the largest species in the genus, the land mullet *Egernia major* (Gray), and to explore its distribution, geographic variation, diet and reproduction.

MATERIALS AND METHODS

All available specimens of *Egernia major* in museum collections in Australia were examined, together with the holotype. Collection abbreviations are as follows: AM, Australian Museum, Sydney; BMNH, Natural History Museum, London; MV, Museum of Victoria, Melbourne; NTM, Northern Territory Museum, Darwin; QM, Queensland Museum; SAM, South Australian Museum.

Head shield nomenclature follows Taylor (1935:71) and Shea (1992, 1995a). Body and limb scalation follows Shea (1995a).

Non-cephalic measurements follow Cogger (1975) and Greer (1982), while cephalic measurements follow Shea (1992, 1995a). Head measurements were made with dial calipers to the nearest 0.1 mm, while other measurements were made with a steel rule to the nearest 0.5 mm. The following abbreviations for measurements are used throughout the text: SVL — snout-vent length; AGL — axilla-groin length; TL — tail length; FLL — forelimb length; HLL — hindlimb length; HL — head length; HW — head width; HD — head depth; EYE — eye diameter; EAR — maximum diameter of ear.

Because of significant allometry, metric data are presented in two forms: the more traditional range of ratios, allowing comparisons with previous studies, and allometric correlations, expressing the degree of allometry and allowing statistical comparisons between sexes and populations.

For the purposes of analysing geographic variation, the overall distribution of the species was divided into discrete subunits (populations) based on apparent discontinuities in the distribution of collecting localities. For metric characters, the effects of allometry were removed prior to analysis by adjusting the log-transformed values to those they would assume if the specimen were of uniform body size (SVL) using the methods of Thorpe (1975) and Shea (1995a). Univariate comparisons between populations were performed by one-way analysis of variance in both meristic and transformed metric characters. Those characters showing significant variation between populations were then included in a canonical variates analysis.

Analysis of variance and covariance, and canonical variates analysis were performed

with SYSTAT Ver 4.0 (Wilkinson 1987). In presenting results of statistical tests, subscripted integers are degrees of freedom, n.s. = non significant result ($p > 0.05$), and the superscripts *, ** and *** indicate significance at $p < 0.05$, <0.01 and <0.001 respectively.

REDESCRIPTION OF *EGERNIA MAJOR*

Egernia major (Gray, 1845a)

Tropidolepisma major Gray, 1845a: pl. 14

Egernia bungana de Vis, 1888: 814.

DIAGNOSIS

The largest species of *Egernia* (SVL up to 301 mm), additionally differentiated from all other *Egernia* species by the following unique character states for the genus: dorsal coloration dark brown/grey; scales above fourth toe paired over most of toe (to at least the base of the antepenultimate phalanx); lower secondary temporal very large (probably incorporating the adjacent tertiary temporals of similar species); posttemporal scales uniformly small, in 2–3 rows between lower secondary temporal and rostral margin of ear. All of these character states are probably autapomorphies of the species, although the supradigital scale state is likely a reversal, as paired supradigital scales are generally primitive for lygosomine skinks (Greer 1979). Other features uncommon in *Egernia* are a low number of midbody scales (28–30), short tail with correspondingly few subcaudal scales (71–77) and nine premaxillary teeth.

DESCRIPTION

External morphology

Nasals broadly to moderately separated; supra- and postnasals not distinct from nasal, though a postnarial groove ventrally partially separates postnasal and nasal; prefrontals usually in broad to moderate contact (50.0%, n = 68), less commonly in narrow (19.1%) or point (19.1%) contact, rarely narrowly separated (8.8%) or with an interposed azygous scale (2.9%); frontoparietals paired; parietals separated by interparietal; nuchals 1–4 ($\bar{x}$ = 3.1, sd = 0.68, n = 136) on each side; a variably-sized azygous occipital usually present (74.6%, n = 67) caudal to interparietal; supraoculars four, first two in contact with frontal; supraciliaries 9–12 ($\bar{x}$ = 10.3, sd = 0.73, n = 133), usually ten (52.6%), last few supraciliaries irregularly divided into an upper and lower series (counts taken from upper series); loreals two, in horizontal series, rostralmost narrower; subocular series of scales complete; presuboculars usually two bilaterally (80.9%, n = 68), rarely one unilaterally (8.8%) or bilaterally (8.8%), or three unilaterally (1.5%); suboculars 1–3 ($\bar{x}$ = 2.0, sd = 0.54, n = 82); postsuboculars 4–7 ($\bar{x}$ = 5.7, sd = 0.54, n = 136), usually six (64.7%); lower eyelid scaly; lobules along rostral margin of ear 3–6 ($\bar{x}$ = 3.8, sd = 0.60, n = 136), usually four (63.2%); primary temporal moderate, usually single, rarely paired unilaterally (n = 1) or bilaterally (n = 1); upper secondary temporal moderate, overlapping lower secondary temporal; lower secondary temporal very large, equivalent in extent to lower secondary temporal plus immediately adjoining posttemporals of other *Egernia* (Figs 1–2); posttemporals between lower secondary temporal and ear very small, thin, in two (17.2%, n = 29) to three (82.8%) transverse series; supralabials usually seven bilaterally (82.4%, n = 68), rarely six unilaterally (8.8%) or bilaterally (2.9%), or eight unilaterally (5.9%); infralabials 8–11 ($\bar{x}$ = 9.0, sd = 0.70, n = 136), usually nine (52.9%); postmental usually contacts first two infralabials on each side (88.0%, n = 67), rarely first only unilaterally (9.0%) or bilaterally

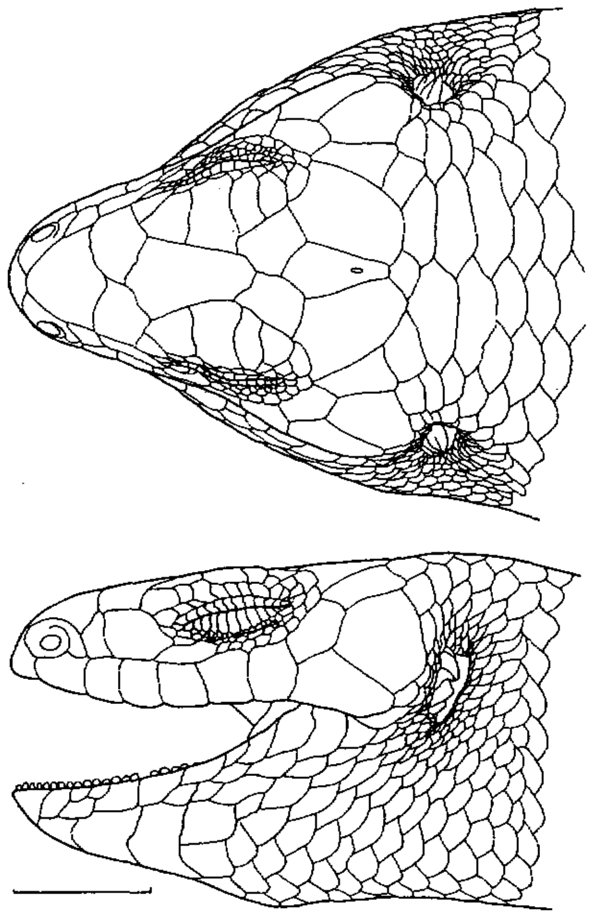

Figure 1. Dorsal and lateral views of the head shields of *Egernia major* (AM R80562). The bulging gular region is an artefact of preservation. Scale bar = 15 mm.

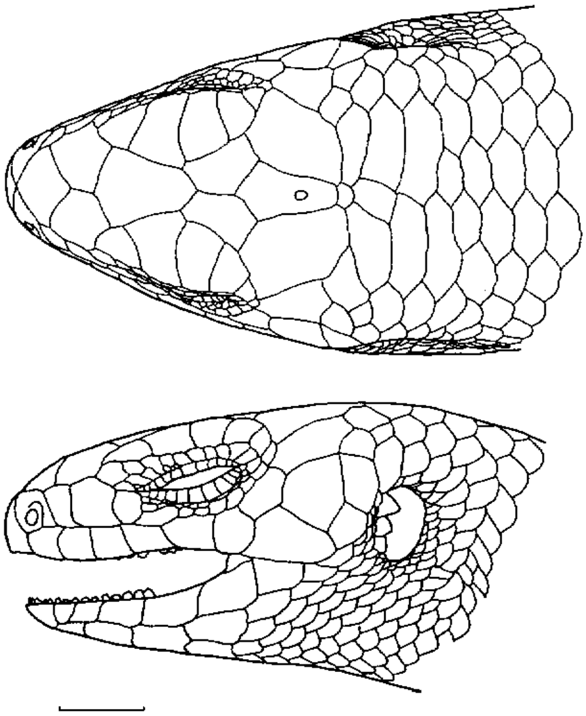

Figure 2. Dorsal and lateral views of the head shields of *Egernia frerei* (AM R66765). Note that the lower secondary temporal and adjacent posttemporals, as in other *Egernia*, cover the same field as the lower secondary temporal of *E. major*. Scale bar = 5 mm.

(3.0%); first pair of chin shields usually entire and contacting medially, rarely divided unilaterally (n = 1) or bilaterally (n = 1), in the latter instance also separated by an azygous scale; second pair of chin shields usually entire, separated by a single scale, rarely divided unilaterally (n = 5) or bilaterally (n = 5) and separated by two scales (n = 1); chin shields of third row usually divided into lateral and medial scales, and separated by three imbricate ventral scales, rarely divided into three scales unilaterally (n = 1) or bilaterally (n = 1) or separated by four scales (n = 1).

Body scales largest dorsally and ventrally, dorsally and laterally with several fine grooves separating very low, blunt keels in adults, smooth in neonates, in 28–30 ($\bar{x}$ = 28.6, sd = 0.86, n = 69) longitudinal rows at midbody; scales in paravertebral row slightly broader than adjacent dorsal scales, 44–48 ($\bar{x}$ = 46.7, sd = 0.98, n = 69) from parietal to level of cranial margin of hindlimb; median row of subcaudal scales a little larger than adjacent scales, 71–77 ($\bar{x}$ = 73.1, sd = 1.51, n = 28); subdigital lamellae broadly rounded, below fourth toe 19–25 ($\bar{x}$ = 21.9, sd = 1.28, n = 117); scales above fourth toe paired from base to at least proximal end of third phalanx, usually to distal end of third phalanx (Fig. 3).

SVL 70–301 mm (n = 69); AGL/SVL (%) 42.5–55.6 ($\bar{x}$ = 49.9, sd = 2.98, n = 67); TL/SVL (%) 105.3–126.9 ($\bar{x}$ = 115.5, sd = 4.86, n = 28); FLL/SVL (%) 22.7–34.0 ($\bar{x}$ = 26.9, sd = 3.44, n = 66); HLL/SVL (%) 31.6–48.6 ($\bar{x}$ = 37.6, sd = 4.10, n = 64); HL/SVL (%) 16.6–25.7 ($\bar{x}$ = 20.1, sd = 2.85, n = 69); HW/HL (%) 66.1–88.2 ($\bar{x}$ = 76.8, sd = 5.70, n = 69); HD/HL (%) 51.9–74.7 ($\bar{x}$ = 61.1, sd = 4.89, n = 69); EYE/HL (%) 20.2–33.5 ($\bar{x}$ = 25.1, sd = 3.64, n = 68); EAR/HL (%) 13.1–21.9 ($\bar{x}$ = 17.7, sd = 1.86, n = 68).

Coloration (in preservative)

Dorsally and laterally glossy dark brown to black. Slightly darker centres to body and tail scales of the palest individuals produce a series of narrow longitudinal dark stripes on most scale rows. Margins of eyelids white. Venter pale, unpigmented, throat with variable development of dark flecks, usually strongest laterally. Change from dark lateral surface to pale ventral surface not abrupt.

Juveniles with a few pale spots laterally on neck and about axilla.

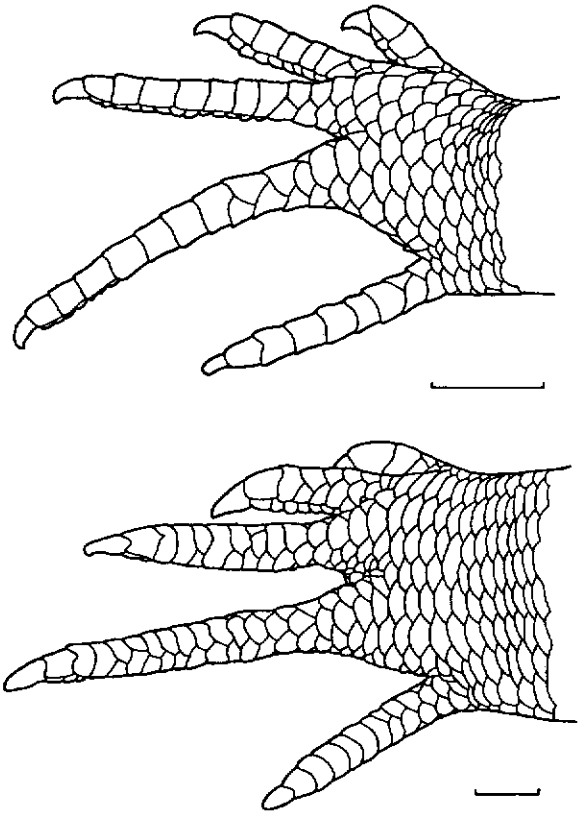

Figure 3. Dorsal view of pes of *E. frerei* (AM R66765; top) and *E. major* (AM R80562; bottom). The former figure illustrates the usual condition for other *Egernia*. Scale bars = 5 mm.

Coloration (in life) (Fig. 4)

Nine live adults examined, eight of which were from the Barrington Tops region, New South Wales, had dorsal and lateral coloration similar to that of preserved material, but venter with a pale straw yellow (n = 4) to mid yellow (n = 5) flush, four of the latter individuals with an orange flush to the throat. The irides were dark brown to almost black, and the tongue and oral cavity pink. The pupil was circular.

Allometry

With respect to SVL, AGL and TL showed positive allometry, while limb lengths and HL showed negative allometry. With respect to HL, HW and HD showed positive allometry, while EYE and EAR showed negative allometry (Table 1). Thus, juveniles have a shorter body, longer limbs, longer but narrower and shallower head and larger eyes and ears than adults.

Sexual dimorphism

No statistically significant differences were detected between males and females in number of nuchals, supraciliaries, postsuboculars, infralabials, midbody scales, paravertebral scales, subcaudal scales or subdigital lamellae (one-way analysis of variance).

Statistically significant sexual dimorphism was detected in the relationship of AGL, FLL and HL with SVL, and of HW and EAR with HL (analysis of covariance, log-transformed data; Table 2). Adult males have slightly shorter bodies but slightly longer forelimbs and heads than adult females, although the degree of dimorphism is minor. Apparent sexual dimorphism at very small sizes may be an artefact of the lack of very small females in the sample analysed.

Slight sexual dimorphism was also apparent in adult SVL (see below, under Reproduction).

Figure 4. A live individual of *Egernia major*.

Table 1. Allometric equations and predicted values for cranial and somatic proportions in *Egernia major*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{70}, C_{250} and C_{300} are predicted proportions at SVL = 70, 250 and 300 mm (minimum, mean of male/female minimum mature and maximum SVL). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{70}	C_{250}	C_{300}
AGL	SVL	1.085	0.321	0.998	0.008	46.1	51.3	52.1
TL	SVL	1.033	0.983	0.998	0.012	113.1	117.9	118.7
FLL	SVL	0.797	0.767	0.997	0.008	32.4	25.0	24.1
HLL	SVL	0.832	0.894	0.997	0.008	43.8	35.4	34.3
HL	SVL	0.779	0.628	0.996	0.009	24.6	18.5	17.8
HW	HL	1.122	0.495	0.996	0.013	70.0	79.0	80.4
HD	HL	1.118	0.399	0.993	0.016	55.8	62.7	63.8
Eye	HL	0.713	0.691	0.986	0.015	30.5	23.0	22.1
Ear	HL	0.854	0.296	0.977	0.023	19.5	16.9	16.6

Table 2. Sexual dimorphism in cranial and somatic proportions in *Egernia major*. Tests of significance (i) and allometric and predicted values for males (ii) and females (iii) in sexually dimorphic characters. Conventions for (ii) and (iii) as for Table 1. C_{70}, C_{250} and C_{300} are predicted proportions at SVL = 70, 250 and 300 mm (approximate minimum, mean minimum mature and maximum SVL).

(i)

		Slopes			Intercepts		
y	x	F	d.f.	P	F	d.f.	P
AGL	SVL	0.017	1,42	n.s.	13.934	1,43	***
TL	SVL	0.003	1,12	n.s.	1.875	1,13	n.s.
FLL	SVL	0.882	1,42	n.s.	7.175	1,43	**
HLL	SVL	2.462	1,41	n.s.	3.523	1,42	n.s.
HL	SVL	0.091	1,42	n.s.	7.575	1,43	**
HW	HL	4.699	1,42	*			
HD	HL	0.107	1,42	n.s.	0.163	1,43	n.s.
Eye	HL	2.762	1,42	n.s.	0.076	1,43	n.s.
Ear	HL	7.378	1,42	**			

(ii)

y	x	a	b	r	s.e.	n	C_{70}	C_{250}	C_{300}
AGL	SVL	1.062	0.360	0.998	0.011	28	46.8	50.7	51.3
FLL	SVL	0.801	0.763	0.997	0.013	28	32.8	25.4	24.5
HL	SVL	0.802	0.563	0.998	0.010	28	24.3	18.9	18.2
HW	HL	1.098	0.544	0.993	0.025	28	71.9	79.2	80.3
Ear	HL	0.885	0.266	0.982	0.034	28	19.2	17.1	16.8

(iii)

y	x	a	b	r	s.e.	n	C_{70}	C_{250}	C_{300}
AGL	SVL	1.057	0.382	0.994	0.029	18	48.7	52.3	52.9
FLL	SVL	0.761	0.920	0.974	0.044	18	33.3	24.6	23.5
HL	SVL	0.815	0.505	0.961	0.059	18	23.0	18.2	17.6
HW	HL	1.253	0.297	0.979	0.065	18	61.0	78.4	81.3
Ear	HL	0.595	0.803	0.798	0.113	18	25.4	17.0	16.0

Osteology and dentition (based on AM R127937, SVL 275 mm) (Fig. 5)

Premaxillae and nasals paired; premaxillary teeth 4L/5R; frontals fused, with exposed maxillary processes long and slender, contacting maxilla; parietal with long caudal descending processes embracing rostral tectal process of supraoccipital; maxillary teeth 21L/20R; ossified palpebrals present, small and rounded; pre- and postfrontals broadly separated along frontal by a distance a little less than width of narrowest point of frontal; postfrontal with long slender frontal and jugal processes, the latter only slightly shorter than the former; postorbital absent; supratemporal large, contacting quadrate; lacrimal present; maxillary process of jugal long, contacts ectopterygoid and lacrimal; caudal process of jugal short, bluntly spinose; temporal process of jugal narrowly separated from squamosal; caudal end of squamosal moderately laterally reflexed, contacting quadrate; quadrate extended laterally, lateral margin in profile with a right angled bend between dorsal and rostral arcs; a prominent rostrodorsal muscular tubercle on rostral face of quadrate; vomers paired, extending between vomerine processes of palatine; ventral laminae of palatines separated medially; lateral palatine canal nearly enclosed; medial palatine canal as a deep groove along dorsomedial surface of dorsal lamina of palatine; medial palatine process of ectopterygoid present and robust, broadly contacting palatine to exclude pterygoid from suborbital vacuity.

Dentary teeth 24; medial lip to dental groove sharp; coronoid and angular processes of dentary long and diverging; portion of Meckelian canal in dentary fully enclosed; Meckelian foramen between splenial and dentary located below centre of dentary tooth row; splenial large, but does not reach caudal process of coronoid; medially exposed portion of rostral process of coronoid extends rostrally below last five teeth, not medially overlapped by dentary; prearticular and surangular fused rostral to Meckelian fossa, but with a groove marking the former position of the suture.

Presacral vertebrae 26; vertebrae at midtrunk longer than wide; sacral vertebrae two, fused; cranialmost autotomy plane on postsacral vertebra 7, passing laterally across craniobasal segment of transverse processes; short cervical ribs on vertebrae 4–6; long cervical ribs on vertebrae 7–8; sternal ribs on vertebrae 9–11; mesosternal ribs on vertebrae 12–13; postsacral vertebra 2 with a pair of ossified hemal pads, subsequent vertebrae with hemal arches.

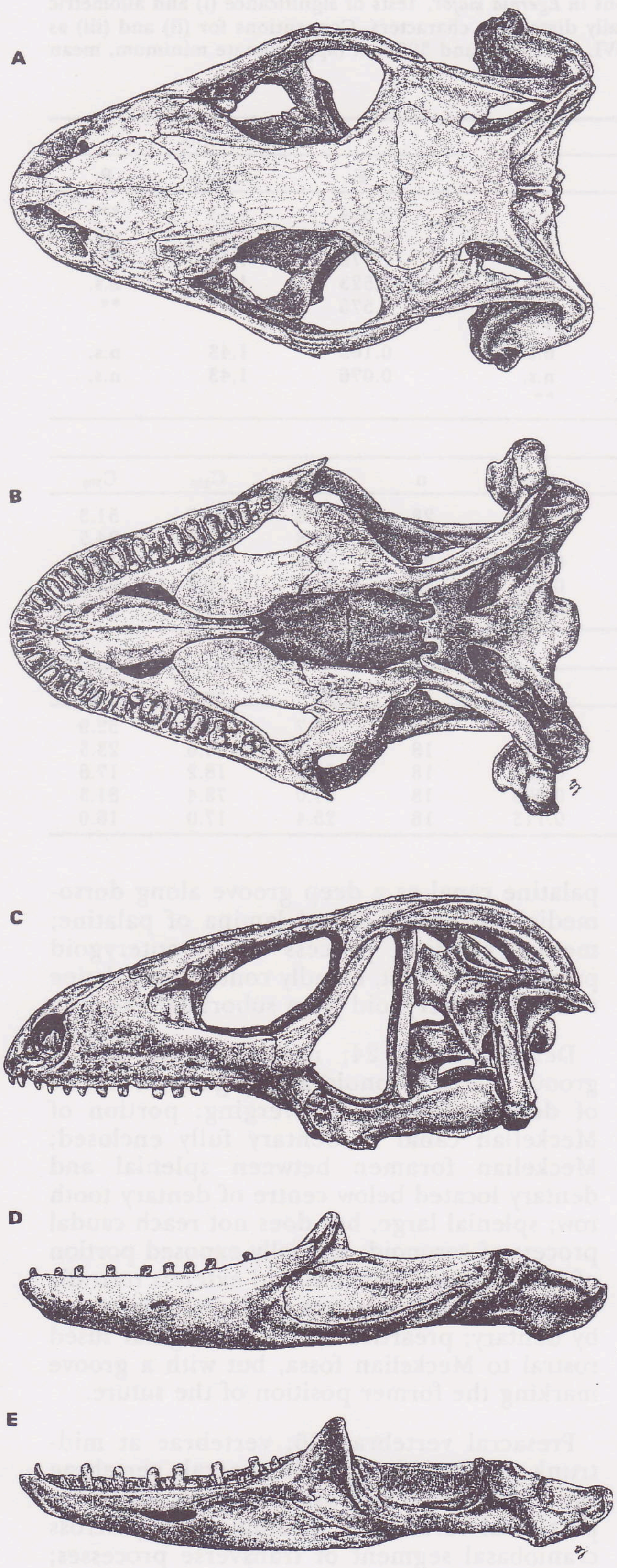

Figure 5. Dorsal (A), ventral (B) and lateral (C) views of skull and lateral (D) and medial (E) views of mandible of *Egernia major* (AM R127937).

Scapular fenestra absent; clavicular fenestra present; intermedium present in carpus; phalangeal formula of manus 2.3.4.5.3.

Wing of ilium not angled to body in lateral profile; phalangeal formula of pes 2.3.4.5.4.

DISTRIBUTION

Egernia major is apparently discontinuously distributed between the Conondale Ranges, Queensland in the north, and the north side of the Hawkesbury River, New South Wales in the south, and occurs at altitudes from sea level (Park Beach, New South Wales) to 840 m (Acacia Plateau, Queensland) (Fig. 6).

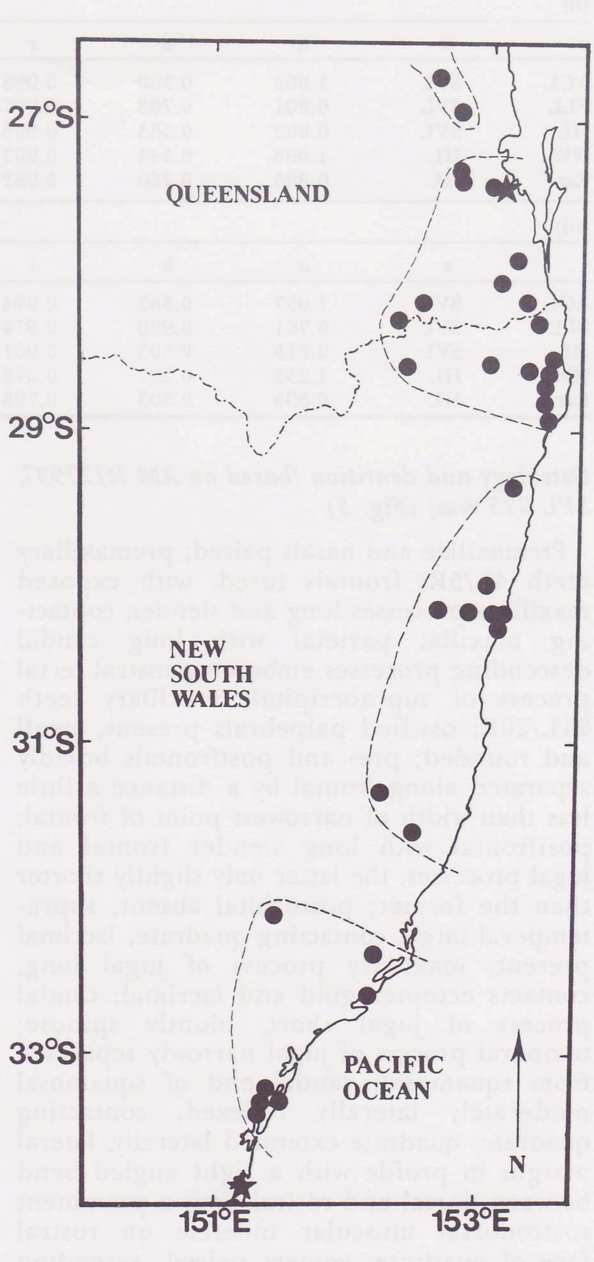

Figure 6. Distribution of *Egernia major*. Dashed lines delimit the groups used in the canonical variates analysis. Stars indicate the position of the cities Sydney (southern) and Brisbane (northern).

Available records show five clusters of localities. From south to north, these are: (1) the Gosford-Ourimbah-Wyong area between the Hawkesbury and Hunter River valleys; (2) the Barrington Tops-Bulahdelah-Myall Lakes area immediately north of the Hunter River valley; (3) the Port Macquarie-Coffs Harbour area between the Hastings and Clarence River valleys; (4) the New South Wales/Queensland border region, from the Richmond River valley north to the D'Aguilar Range, and (5) the Conondale Ranges.

One old locality, Tamworth, New South Wales (AM R2219) is considered erroneous. This locality is in dry woodland not otherwise inhabited by the species, is not supported by more recent collections from the area, and is part of a large collection of reptiles from a variety of localities purchased from D. A. Porter and known to include other anomalous localities (pers. obs.).

GEOGRAPHIC VARIATION

Four geographically discrete populations were used in considering geographic variation. The two southern groups were combined into one population due to the very small sample available for the second group (n = 3). The four resulting groups are referred to in this section as Southern, Central, Northern and Conondale populations.

Analysis of variance revealed no significant differences among these four groups in number of paravertebral scales, subcaudal scales, subdigital lamellae, postsuboculars, or the following adjusted measurements: FLL, HLL, HW, HD, Eye, Ear. Significant differences were detected between the populations in the following six characters: midbody scales ($F_{3,60}$ = 3.819*); infralabials ($F_{3,59}$ = 4.260**); supraciliaries ($F_{3,58}$ = 4.173**); nuchals ($F_{3,59}$ = 3.536*); adjusted AGL ($F_{3,59}$ = 4.650**) and adjusted HL ($F_{3,59}$ = 4.267**).

A canonical variates analysis (Fig. 7) using these six characters across the four groups correctly identified only 58% of the 62 individuals (Southern: 40%, n = 10; Central: 73%, n = 11; Northern: 56%, n = 34; Conondale: 71%, n = 7). Using the scores derived from the first canonical function, which was derived largely from midbody scales, supraciliaries and head length, clinal variation was apparent in populations north of the Hunter River valley (Fig. 8), while individuals from south of the Hunter River had scores within the range of the Northern population.

Among the individuals used in the analysis were two litters with their female parents. One litter and parent from the Conondale population had Function I scores from 0.86 to 2.45 (n = 4; span 1.60), while a second litter and parent from the Northern population had Function I scores from –0.82 to 1.57 (n = 8; span 2.39). These ranges did not include the extreme values for their populations, but spanned respectively 29% and 65% of the overall range of scores for their populations.

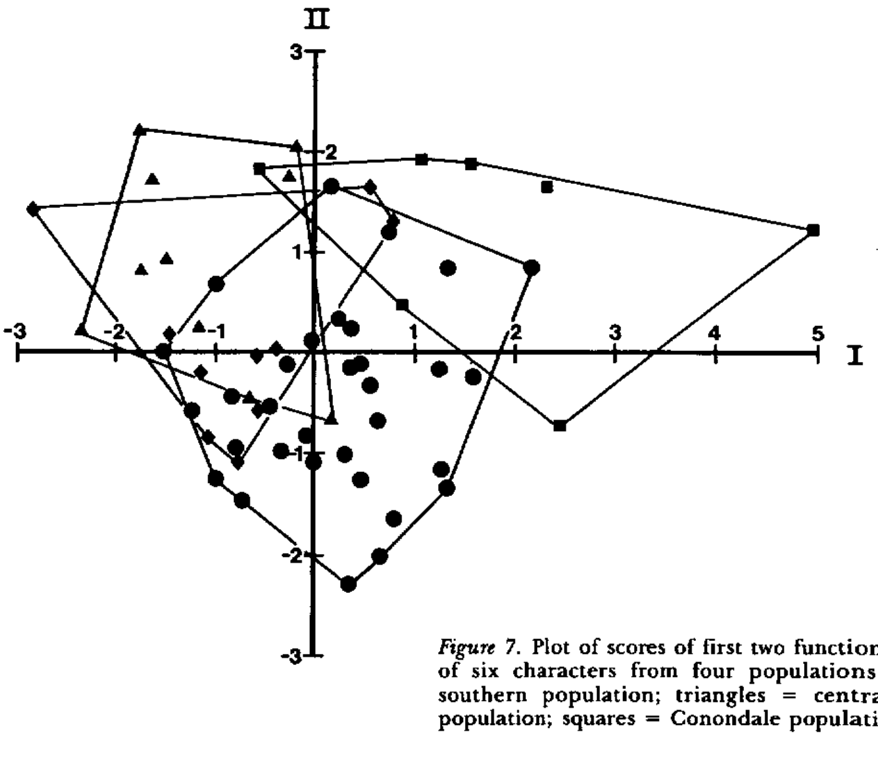

Figure 7. Plot of scores of first two functions from canonical variates analysis of six characters from four populations of *Egernia major*. Diamonds = southern population; triangles = central population; dots = northern population; squares = Conondale population.

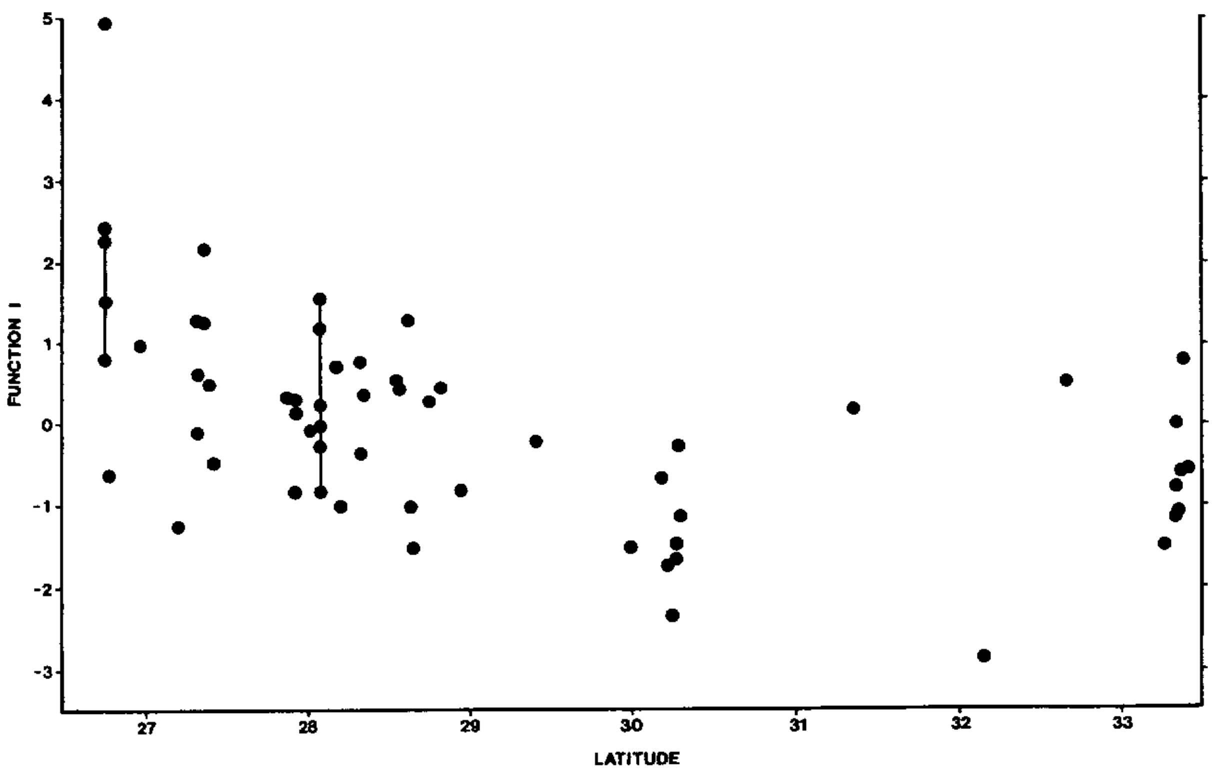

Figure 8. Plot of scores derived from first canonical function against latitude. Bars join scores for two females and their litters.

The results of the canonical variates analysis do not provide any evidence for geographically distinct morphotypes within *Egernia major*.

TAXONOMIC HISTORY AND TYPE MATERIAL

The name *Tropidolepisma major* was published twice in the same year by Gray (1845a,b). The earlier appearance (February 1845; Adler 1995) was as the caption to plate 14 in the herpetological section of the zoological report of the British Antarctic Expedition (Gray 1845a). Unfortunately, funding difficulties resulted in extensive delays in publication (Shea 1995b), and only the initial eight pages of text for the herpetological account, which did not include the written description of *T. major*, were ever published.

A description of *Tropidolepisma major* was published by Gray (1845b) (published 28 June 1845; Sherborn 1926), who referred to a single stuffed and mounted specimen from "Australia", and cited Gray's (1845a) plate. The description is typically brief, stating "dark olive, chin and beneath whitish; scales very large, broad, smooth, in 8 series on the back, each with 3 slightly raised distinct smooth parallel keels, of the tail similar but rather larger, of the upper part of the legs nearly smooth; tail elongate."

The publication of a labelled plate prior to 1930 constitutes a valid description of a new species (Code of Zoological Nomenclature Article 12(b)(7)), and hence Plate 14 in Gray (1845a) must be considered the type description of the species, and the single specimen illustrated is the holotype.

Duméril and Duméril (1851) provided a more extended, though still brief, description of *T. major*, including the first measurements, based on three specimens collected by Jules Verreaux at the Moreton Bay settlement.

Gray (1867) republished the illustration of *Tropidolepisma major* under the name *Tropidolepisma majus*, ascribing the name to Gray (1845b), and the unjustified emendation of the specific epithet to Günther, his assistant at the British Museum. Günther (1875), in a revised list of the lizards of Australia and New Zealand accompanying the publication of the full set of herpetological plates for the Antarctic Expedition report, restricted the distribution of the species to eastern Australia, giving the localities Sydney and Rockhampton. Cogger *et al.* (1983) considered these localities to represent a restriction of the type locality of the species. However, I consider that Günther's listing refers to additional specimens received by the British Museum subsequent to the description and ascribed to the species.

The Natural History Museum in London, which received the zoological collections of the British Museum, has only four large eastern Australian *Egernia* registered prior to 1875: the holotype of *T. major* (xv.88a), a second stuffed and mounted specimen of *E. major* (56.12.3.5) from Australia, purchased from Mr Cuming, a halfgrown specimen of *E. major* (63.6.16.27) from Australia, donated by Gerard Krefft, who was based in Sydney, and a single specimen of *Egernia rugosa* (67.5.6.66) from Rockhampton, purchased from Mr Higgins. The latter species was undescribed when the specimen was registered, and was identified as *E. major* at the time (Günther 1867).

Without further comment, Günther (1879) subsequently identified lizard specimens from the islands of Torres Strait as *T. majus*, although he had previously (Günther 1877) identified material from the same source as *T. striolatum* Peters 1870.

Boulenger (1887) synonymised *Tropidolepisma* with *Egernia*, and assigned to *E. major* seven specimens from Torres Strait and "Australia". Despite his reidentification of the Rock-hamption record, his redescription of *E. major* was still composite, with the Torres Strait specimens referrable to *E. frerei* Günther 1897. His description of coloration in particular is largely based on the more colourful *E. frerei*, as is the set of measurements given.

In the following year, de Vis (1888) reported the occurrence of two species of large *Egernia* in the Brisbane area. The smaller more colourful, striped species from "low grounds in the vicinity of water" he identified as *E. striolata* (Peters), while the larger dark species from the "mountain scrubs" he described as *Egernia bungana*. Presumably on the basis of the measurements provided by Boulenger, de Vis reported that *E. bungana* grew to a much larger size than *E. major*.

De Vis' *E. striolata* is almost certainly *E. frerei*, at the time undescribed. De Vis' confusion is understandable, as he would have been relying on the descriptions of Peters (1870) and Boulenger (1887), which fit both species. De Vis apparently recognized the distinction between *E. striolata* and *E. frerei*, although misapplying the former name, as a series of specimens of *E. striolata* in the Queensland Museum (J13752–70) bears a de Vis manuscript name, *Tropidolepisma rufiventris*.

The combination of Boulenger's composite description of *E. major* and de Vis's description of *E. bungana* led to an extended period of taxonomic confusion. For over 90 years, herpetologists applied the name *E. major* to the smaller colourful species, and *E. bungana* to the larger dark species. This was exacerbated by the description of *E. frerei* by Günther (1897). Although Günther (1877, 1879) had previously seen Torres Strait material now ascribed to that species, he noted that *E. frerei* was "certainly distinct from all which I know by autopsy, and cannot be referred to any of the other described species . . .". The holotype of *E. frerei* is lost (Cogger *et al.* 1983), and in its absence, later authors (Mitchell 1950; Worrell 1963) treated it as distinct from both *E. major* and *E. bungana*.

Longman (1918) and Loveridge (1934), working with limited material, were suspicious of the constancy of the minor differences in scalation between *E. bungana* (= *E. major*) and *E. major* (= *E. frerei*). Loveridge (1934) suggested that the differences in size and coloration may be due to age, but tentatively followed Longman in retaining the two as distinct.

Mitchell (1950), working with two specimens he identified as *E. major* and two as *E. bungana*, reported several (unspecified) scalational differences between the two taxa, but in the absence of additional confirmatory material was reluctant to recognize them. Ignoring de Vis' identification of both species from the Brisbane area, Mitchell treated *E. bungana* as a subspecies of *E. major*. Worrell (1963) reported broad sympatry of the two taxa in southern Queensland and northern New South Wales, and treated them as distinct species, although following contemporary usage in the application of the names.

Cogger (1975) followed Worrell (1963) in recognizing two species, but applied the name *E. major* to the large dark species and *E. frerei* to the smaller colourful species. This action was based on Cogger's examination of the holotype of *T. major* in 1970, but was not formally justified until 1983 (Cogger *et al.* 1983).

The holotype of *T. major* (BMNH xv.88a; Fig. 9) agrees in all respects with the species to which the name was applied by Cogger (1975) and which is here redescribed. It is an adult stuffed and mounted on a board. The board bears on the front the annotation: "Large Tropidolepisma/*Tropidolepisma major*/ Australia", while the underside bears the annotation "Feb 1837/*Tropidolepisma major*/ xv88a/Type/Original description and fig. in Voy. of Erebus and Terror Fig Pl./*Egernia major*".

I am reluctant to accept the February 1837 date for four reasons. Firstly, the reference to

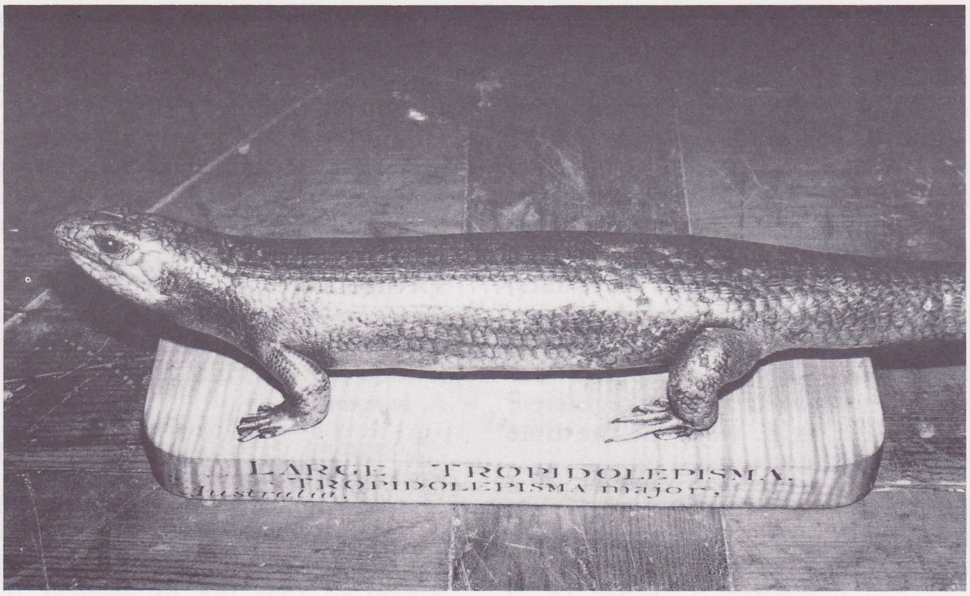

Figure 9. Holotype of *Egernia major* (BMNH xv.88a).

the Voyage of the *Erebus* and *Terror* cannot have been added before 1845. Secondly, the February 1837 date appears on the similarly mounted types of *Hinulia gerrardii* Gray 1845 (now *Cyclodomorphus gerrardii*), yet neither of these distinctive species is noted in two major catalogues by Gray (1838, 1841) prior to his 1845 description. Both catalogues were intended to be comprehensive and included or were associated with the description of numerous new species and genera of Australian lizards. If these two species were present in the British Museum collection by 1837, it is inconceivable that Gray would have failed to notice them. Thirdly, the same date appears on another mounted specimen of problematic age: the purported lectotype of *Hydrosaurus gouldii* Gray 1838, recorded as having been obtained from John Gould, who did not reach Australia until 1838 (Whittell 1954). Fourthly, the known distribution of *E. major* was poorly explored and almost unsettled prior to 1837. By 1845, however, several settlements in the Brisbane area had been founded, and logging of northern New South Wales forests was actively proceeding.

The holotype has SVL 268 mm, AGL 153 mm, tail regenerated, but proximal 302 mm original; HL 46.9 mm; HW 36.9 mm; HD 30.7 mm; nasals broadly separated; prefrontals in point contact; two presuboculars; 6/5 postsuboculars; ten supraciliaries; seven supralabials; eight infralabials; 3/4 nuchals; three rostral ear lobules; midbody scales at least 26 (accurate count not possible due to the form of the mount and damage to the venter during skinning and stuffing); paravertebral scales 47. There are a number of small holes, possibly shot holes, about the caudal part of the body, and a few similar holes around the neck.

No types were nominated for *Egernia bungana* by de Vis, and no specimens have been subsequently identified as types (Covacevich 1971; Cogger *et al.* 1983). De Vis was evidently familiar with the species, noting habitat preferences and an Aboriginal name (bungan), and probably had access to more than one individual, although only a single set of scale counts and measurements are presented. The locality "S. Queensland" given is probably more a statement of distribution than a specific type locality. All characters noted by de Vis are within the range of variation known for *E. major*. In particular, the coloration and size (SVL presumably 297 mm, from total length 665 mm, tail length 368 mm) are autapomorphies of the species and clearly identify the taxon.

The common name "Land Mullet" applied to this species dates back to Longman (1918), who reported it to be in common usage for the species around Tambourine Mountain. The name probably alludes to the superficial resemblance to the homonymous fish, which has a similarly blunt head, large scales and is of similar size and coloration.

COMPARISON WITH OTHER *EGERNIA* SPECIES AND RELATIONSHIPS

The large size and uniform dark coloration of *Egernia major* readily separate it from all other *Egernia* species. Only some *E. kingii* share large size and dark coloration, and could be confused with *E. major* on a cursory

inspection. However, *E. kingii* has strongly keeled dorsal and lateral body scales, paired supradigital scales only on the base of the fourth toe, 32 or more midbody scales and usually eight or more supralabials (Storr 1978), lacks the very large lower secondary temporal scale of *E. major* and has larger posttemporal scales.

In a phenetically-based discussion of relationships in *Egernia*, Horton (1972) considered *E. major* to be related to two other large *Egernia* species: *E. frerei* and *E. rugosa*. One additional large *Egernia* similar to *E. frerei* has subsequently been described (*E. obiri* Wells and Wellington 1985; see also Sadlier 1990, as *E. arnhemensis*). The character states used by Horton to delimit this group, the *E. major* group, are large size, multiple pairs of nuchal scales, keeled dorsal scales, burrow construction and omnivory. All of these character states are shared with *E. kingii*, which Horton identified as a distinct monotypic group, several are also shared with other groups within *Egernia*, and most are plesiomorphic. Further, the integrity of the *E. major* group was contradicted by Horton's "summary of species relationships" (Horton 1972: 107), which pairs *E. bungana* (= *E. major*) and *E. dorsalis* (= *E. rugosa*) at the top of the tree, while *E. major* (= *E. frerei*) is at the bottom of the tree.

Preliminary studies of morphological variation in *Egernia* do not reveal any synapomorphies linking the four species in the "*E. major* group", and the relationships of *E. major* are best considered unresolved.

REPRODUCTION

The smallest apparently mature female (well-developed, pleated oviducts; large ovarian follicles) had SVL = 269 mm. Females of this size and larger were assumed to be mature, and had SVL 269–299 mm ($\bar{x}$ = 285.0 mm, sd = 9.23 mm, n = 15). The smallest apparently mature male (enlarged, turgid testes; opaque convoluted ductus deferens) had SVL = 247 mm. Males of this size and larger were assumed to be mature, and had SVL 247–301 mm ($\bar{x}$ = 274.4 mm, sd = 15.57 mm, n = 21).

Minimum size at maturity may be smaller, as the material examined included only one female with SVL between 203 and 268 mm, and one male with SVL between 148 and 246 mm.

There is a significant difference between the sexes in adult SVL (Wilcoxon Rank-Sum test; z = 2.15*), with females generally larger.

The mature sex ratio (16:21, including one large but headless female not included above) was not significantly different to 1:1 (χ^2_1 = 0.68, n.s.).

Litter sizes were available for seven of the mature-sized females. In chronological order, QM J41381 (SVL indeterminate; collected 10.x.1979) contained 2L/3R yolking ovarian follicles, up to 17.5 mm diameter; QM J47395 (SVL 285 mm, collected xi.1987) contained 3L/3R oviducal yolk masses; QM J55212 (SVL = 275 mm, collected 6.ii.76) contained 3L/3R pigmented embryos; AM R70428 and R70429 (SVL = 280 mm, 270 mm respectively, both euthanased 15.ii.78) contained 2L/1R and 1L/2R pigmented oviducal embryos; QM J8498 (SVL = 295 mm, collection date not recorded) gave birth to seven young (QM J8487, J8489, J8491, J8493, J8495–97), all registered iii.1953 (probably soon after birth), while AM R102980 (SVL = 285 mm, collected 5.i.1981) gave birth to three young (AM R97860–62) on an unspecified date.

The relationship between litter size and maternal SVL was not significant (r = 0.532, $F_{1,4}$ = 1.576, n.s.), although a trend towards larger litters from larger females was apparent.

Of the two litters born in captivity, SVL for the litter of seven was 73–78 mm, $\bar{x}$ = 75.1 mm, sd = 1.77 mm, and for the litter of three was 77–79.5 mm, $\bar{x}$ = 78.5 mm, sd = 1.32 mm. These values are comparable with two other neonates, QM J54537 (died in captivity at 2 days old; 11.ii.1992) with SVL = 82 mm, and AM R6909 (born at Taronga Zoo 16.ii.1916) with SVL = 75 mm, and with another wild-caught individual from the same month (QM J33165, 28.ii.1976, SVL = 83 mm). The two smallest specimens examined, AM R66122 (SVL = 72 mm) and AM R66125 (SVL = 70 mm) lack dates of collection or birth. These data suggest that neonates have SVL about 70–80 mm.

Together, the data on occurrence of ovarian follicles and oviducal young with dates of birth suggest that ovulation occurs in October (mid-spring) and 3–7 ($\bar{x}$ = 4.7, sd = 1.70, n = 7) young are born in February (late summer), following a gestation period of 3.5–4 months.

Few data are available for mature males. However, AM R103081 (collected 17.x.1991) had noticeably enlarged turgid testes, compatible with spring spermiogenesis.

The data presented here are consistent with the few previous reports. Longley (1946) reported purchasing two of a litter of nine born to a female being transported to a dealer. This litter is larger than those reported here. As it is not reported first-hand, I am inclined to doubt the size of this litter,

and suggest that more than one female may have been involved. Swan (1990, 1995) and Ehmann (1992) similarly report a maximum litter size of nine, probably based on Longley's record, although their minimum litter (two and four, respectively) approach the figures of this study. Hauschild and Gassner (1995) report a captive-bred litter of two, following about four months gestation. The offspring grew to 152 g and 29 cm (presumably total length) in ten months, and 320 g and 37 cm in the second year.

LONGEVITY

Egernia major is long-lived. From captive studies, Bowler (1977, as *E. bungana*) reported a lifespan of eight years seven months, Swan (1990) reported a lifespan of over eleven years, and Hauschild and Gassner (1995) cite a female held for 23 years. Of two animals held by the author, one was collected as a juvenile in 1982 and died as a result of an accident in December 1997 without showing any signs of excessive age, while the other was collected as an adult in December 1988, and is still alive at the time of writing.

DIET

Identifiable gut contents were present in five of the specimens examined, and these data are supplemented by a fecal pellet obtained from a field-caught animal and two field observations. The stomach of AM R19072 (Tooloom, New South Wales) contained several berries, seeds and pieces of fungal fruiting bodies, together with a giant king cricket (*Australostoma australasiae*; Stenopelmatidae) and a beetle (*Cnemoplites* sp.; Cerambycidae). The colon of the same specimen contained three beetles (*Cephalodesmius armiger*; Scarabeidae: Scarabeinae), together with the remains of a bee, a large orthopteran, probably a katydid (Tettigoniidae), and a leaf. The intestine of AM R107589 (Wardell, New South Wales) contained a mass of fleshy vegetable material, apparently the fruiting bodies of several different woody fungi, together with a grass-hopper head and a 6 mm ovoid seed. The stomach of QM J17913 (Mt Glorious, Queensland) contained the fruiting bodies of several gilled mushrooms. The stomach of QM J35345 (Mafeking Road, near Federal, New South Wales) contained portions of the fruiting bodies of one woody fungus and several softer fungi and other unidentifiable plant material, together with a scarab beetle (Scarabeidae: Melolonthinae). The stomach of QM J47395 (Mt Nebo, Queensland) contained the caps of two soft bolete-type mushrooms, together with portions of other fungi, a piece of moss and a semi-slug (*Helicarion virens*; Helicarionidae). The fecal pellet, from an individual from Barrington State Forest, New South Wales, contained portions of plant stems and arthropod chitin. Two adults (Chichester State Forest, New South Wales, A. Greer, pers. comm.; Lamington National Park, Queensland, P. Harlow, pers. comm.) have been observed eating mushrooms.

These data indicate that *E. major* is omnivorous, like other large *Egernia* (Shea 1995c and references therein). Unusual features of the data are the high frequency of fungi, and the nocturnal nature of several of the animal remains (the king cricket and cerambycid beetle from the colon of AM R19072 and the semi-slug from J47395). Nocturnal prey agrees with the author's observations on two captive animals, which were frequently found either active or sleeping in an open situation at first light.

The data from this study agree with the limited data on diet available from other studies. Conran (1983) reported seeds of cockspur *Maclura cochinchinensis* in the stomach of a wild-caught individual, while Schulz and Eyre (1997) commonly observed wild individuals feeding on fungi, as well as overripe fruit from a compost heap. Captive animals have been reported to eat a range of arthropods, molluscs, annelids, meats and fruits (Longley 1946; Hauschild and Gassner 1995).

SPECIMENS EXAMINED

Conondale Ranges region, Queensland: AM R97860–62, R102980, Conondale Ranges; QM J3175, Woodford; J33165, Sandy Creek, Conondale Range; J55212, Bellthorpe State Forest.

Border region: AM R6197, Tweed River?; R19072, Tooloom, New South Wales; R46069, R91938, QM J23700, J24139, Mt Glorious, Queensland; AM R46070, Booyong, New South Wales; R76103, about 3 km NNE Kyogle, New South Wales; R78366, Red Scrub Flora Reserve, Whian Whian State Forest, New South Wales; R91936, 1mi. E Teviot Falls, Killarney-Boonah Road, Queensland; R107589, Wardell, New South Wales; R132775, vicinity of Alstonville, New South Wales; R134979, Mullumbimby, New South Wales; MV D8588, Murwillumbah, New South Wales; QM J1776, Enoggera, Queensland; J3030, J3044, J6831, Tambourine Mtn, Queensland; J6103, Tambourine North, Queensland; J7598, Acacia Plateau, Queensland; J8487, J8489, J8491, J8493, J8495–98, Cainbable Range, via Canungra, Queensland; J17913, about 1 km from Jolly's Lookout, Mt Nebo, Queensland; J25381, J41381, J47395, Mt Nebo, Queensland;

J35345, Mafeking Road, near Federal, New South Wales; J47331, Mt Nebo area, Queensland; J54537, Purlingbrook Falls National Park, Queensland.

Coffs Harbour region, New South Wales: AM R9015, Comboyne Plateau; R43577, R66127, Coffs Harbour; R66124, R66126, Park Beach, Coffs Harbour; R70428, Sherwood Forest; R70429, Korora; R76096, Mills Road, just east Nymboida River, Wild Cattle Creek State Forest; R91179, north side Clarence River, 3.4 km west Pacific Hwy; R103081, Hastings River, base of Mt Kokamerican; R142002, Lowanna; MV D51937, Bucca Road.

Southern region, New South Wales: AM R12044, Wyong district; R29961, NTM R1137, Ourimbah; AM R66121, Bulahdelah State Forest; R66122–23, The Entrance; R66125, Bateau Bay; R80562, Barrington Guest House; R127376, near Hawks Nest turnoff on Seal Rocks Road, Myall Lakes; NTM R769, Gosford.

Others: AM 4856, ?; R2219, Tamworth, New South Wales; R6909, born at Taronga Zoo; BMNH xv.88a, Australia; MV D8617, central Queensland; SAM R44558, Queensland.

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Book Reviews — Book Reviews

Forests and their environment by T. Sadler, 1993. Cambridge University Press, Cambridge and CSIRO.
ISBN 0 521-43786-5.
RRP $9.95.

This book is one of a series "Science and our Future" developed with CSIRO to provide secondary schools with "accurate, relevant and up-to-date information in fields of science that will have a major impact on our future".

Forestry issues have achieved a high political and media profile in Australia. Is it possible to do justice to the issues and explain the underlying science in a way that is intelligible to the intended audience in a slim volume of 88 pages? My preconception was — "no way" — but I have been pleasantly surprised that my expectation has not been met.

Tony Sadler has been able to provide a succinct introduction to many aspects of forests and forest management in Australia as well as brief introduction to wood technology. The discussion is wideranging, and covers topics such as fire management, pest and diseases, forest ecology and forests and the greenhouse effect. The coverage of environmental issues is brief, and while it includes a photograph of protesters does not address many of the more complex issues associated with wilderness or assessment of conservation values. The only error I noted was a statement "beehives are now excluded from conservation reserves because the introduced honey-bee is not considered a desirable species in such areas" — obviously successive Ministers for the Environment in New South Wales have been of a different view!

The book is a remarkable achievement of clear condensed writing — it would be easy to point to areas where arguments could be extended but few authors would manage to pack so much into so few pages and yet still end up with an enjoyable read.

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